

Preliminary investigation of flexibility in learning color-reward associations in gibbons (Hylobatidae)

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1 Preliminary investigation of flexibility in learning color-reward
2 associations in gibbons (*Hylobatidae*)

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ABSTRACT

Previous studies in learning set formation have shown that most animal species can learn to learn with subsequent novel presentations being solved in fewer presentations than when they first encounter a task. Gibbons (*Hylobatidae*) have generally struggled with these tasks and do not show the learning to learn pattern found in other species. This is surprising given their phylogenetic position and level of cortical development. However, there have been conflicting results with some studies demonstrating higher level learning abilities in these small apes. This study attempts to clarify whether gibbons can in fact use knowledge gained during one learning task to facilitate performance on a similar, but novel problem that would be a precursor to development of a learning set. We tested 16 captive gibbons' ability to associate color cues with provisioned food items in two experiments where they experienced a period of learning followed by experimental trials during which they could potentially use knowledge gained in their first learning experience to facilitate solution of subsequent novel tasks. Our results are similar to most previous studies in that there was no evidence of gibbons being able to use previously acquired knowledge to solve a novel task. However, once the learning association was made, the gibbons performed well above chance. We found no differences across color associations, indicating learning was not affected by the particular color / reward association. However, there were variations in learning performance with regard to genera. The hoolock (*Hoolock leuconedys*) and siamang (*Symphalangus syndactylus*) learned the fastest and the lar group (*Hylobates sp.*) learned the slowest. We caution these results could be due to the small sample size and because of the captive environment in which these gibbons were raised. However, it is likely that environmental variability in the native habitats of the subjects tested could facilitate the

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46 evolution of flexible learning in some genera. Further comparative study is necessary in order to
47 incorporate realistic cognitive variables into foraging models.

48 **INTRODUCTION**

49 Despite being the most diverse group of extant apes, gibbons continue to be the most
50 understudied of all higher primates, particularly with regard to their cognitive abilities. Gibbons
51 are native to South East Asia and can be found in Vietnam, Cambodia, Thailand, Burma, China,
52 Malaysia, and the islands of Indonesia. They are omnivores and in ideal resource availability
53 conditions, high-energy fruit constitutes the majority of their diet with the remainder consisting
54 of leaves, flowers, seeds, tree bark, insects, small birds, eggs and tender plant shoots [Curran &
55 Leighton, 2000]. These small arboreal apes primarily live in monogamous pairs with their
56 associated offspring and are characterized by limited sexual dimorphism, complex vocal duets
57 between the male and female bonded pair and brachiating mode of locomotion [Cunningham &
58 Mootnick, 2009].

59 Representing an interesting evolutionary divergence between monkeys and great apes, a
60 better understanding of gibbon learning ability and their capacity for complex mental processes
61 would allow us to track both the progression of advanced cognition and the evolutionary
62 pressures that have led to the emergence of abilities characteristic of great apes (including
63 humans). This research therefore aims to investigate whether gibbons are able to learn sequential
64 color-reward associations and if they can extract relevant information from the first stimulus-
65 response association to enable them to make future associations more readily.

66 Research on gibbon vision has shown there are separate M and L photo pigments and
67 other characteristics that are almost identical to those of the common chimpanzee (*Pan*
68 *troglydtes*) – known to have trichromatic color vision, suggesting their searching behavior is

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3 69 heavily guided by vision. As all genera of gibbon enjoy the benefits of full trichromatic color
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6 70 vision [Deegan & Jacobs, 2001; Jacobs, 1993; Jacobs, et al., 1996], they should easily
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8 71 discriminate color information from the cues provided during this series of studies.
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10 72 Experimental tests of associative learning in non-human primates in a controlled setting
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12 73 typically employ object discrimination tasks where the subject is presented with two arbitrary
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14 74 shapes, one that if chosen will lead to a reward and one that will not. For example, selection of
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16 75 the red square would lead to reinforcement whereas selecting the blue triangle presented with it
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18 76 in a two-way choice paradigm would leave the subject unreinforced. Data are collected on the
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20 77 number of trials needed to reach a pre-determined criterion level that is assumed to result from
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22 78 the subject learning the rules of the task; that is, which of the two shapes will lead to
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24 79 reinforcement.
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29 80 Using this basic paradigm, Harlow [1949] postulated that rhesus macaques (*Macaca*
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31 81 *mulatta*) made more than a simple association between stimulus and reinforcement, suggesting
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33 82 ‘cognitive mediation’ occurred as subjects learned subsequent stimulus – reward associations
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35 83 more quickly. This seemed to indicate they were extracting some level of information from their
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37 84 first learning experience that they used to inform their actions in novel configurations. This has
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39 85 since been termed ‘learning to learn’ or ‘learning set formation’ [Rumbaugh & McCormack,
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41 86 1967].
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46 87 Since the early observations by Harlow, studies of learning set formation have shown that
47
48 88 many species including rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*),
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50 89 can in fact ‘learn to learn’ with subsequent problems being solved in fewer presentations
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52 90 [Passingham, 1981; Fobes & King 1982]. However, gibbons have typically struggled with these
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54 91 tests that require the subjects to solve different sets of similar problems over time and do not
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92 show the learning to learn pattern found in other species [Rumbaugh & McCormack, 1967;
93 Tomasello & Call, 1997; Abordo, 1976].

94 In the Rumbaugh and McCormack study [1967] five immature gibbons (*H. lar* N=2, *H.*
95 *moloch* N=1; *H. pileatus* N=2) were presented with a simple discrimination task that required
96 subjects to push bins marked by a red square (reinforced) or a red circle (unreinforced) to reveal
97 a reward beneath the reinforced shape. The gibbons had a tendency not to push the bins at all –
98 taking upwards of 100 trials to acquire this basic motor action when compared to other primates
99 tested. However, once they were reliably making a choice, the gibbons did not appear to find
100 learning the discrimination any more difficult than the other apes and monkeys tested (*Pongo*,
101 *Gorilla*, *Pan Sp.*, and *Macacca*) [Rumbaugh & McCormack, 1967]. Unlike the other monkeys
102 and apes, when novel shape pairs were presented, gibbons seemed to learn each new association
103 as a completely new problem, taking the same number of trials to reach criterion performance as
104 they had for the first stimulus pair. Other species took fewer trials to learn each new association
105 suggesting they were using information gained during their first learning experience to inform
106 their choices on subsequent novel presentations. This seemed to be beyond the capacities of the
107 gibbons tested.

108 Other studies have provided contrasting results; for example, in a learning reversal study
109 (where the rewarded shape in a paired association task is ‘reversed’ once the subject reaches
110 criterion performance), Gosette [1970] reported gibbons (*H.lar*) did show evidence of learning to
111 learn making fewer errors than squirrel monkeys (*Saimiri* sp.) and owl monkeys (*Aotus* sp.), but
112 being inferior to capuchins (*Cebus* sp.). As some prior studies have found gibbons generally
113 struggle with learning set formations [Rumbaugh & McCormack, 1967] while others have shown
114 conflicting evidence with better performance [Gosette, 1970], we were interested in clarifying

115 whether gibbons can use knowledge gained during one learning task to facilitate performance on
116 a similar but novel problem that would be a precursor to learning set formation.

117 Gibbons are large-brained primates with their relative brain size being comparable to the
118 great apes and large-brained monkeys [Cunningham & Mootnick, 2009]; therefore, their reported
119 poor performance on discrimination tasks and little evidence of learning set formation is
120 surprising. Several gibbon behavioral characteristics could explain their apparent lack of
121 abilities and contradicting results of previous studies. Gibbons have notoriously short attention
122 spans [Fedor et al., 2008] potentially losing interest after only a few trials, impeding learning set
123 formation. Also, gibbons rely heavily on their visual cognitive abilities - it has been found that
124 gibbons are competent in detecting the visual orientation of other species as well as their own
125 and possess some knowledge of how visual gaze direction relates to external stimuli [Horton &
126 Caldwell, 2006]. Therefore, results will be inconsistent if a subject with a short attention span
127 becomes distracted by a visual cue outside of the experiment.

128 The aim of this study was to determine whether gibbons could learn to associate preferred
129 foods with colored signals when the food items were hidden out of direct sight and once learned,
130 whether they could use their acquired learning to facilitate future learning. That is, once they had
131 learned a particular stimulus-reward association, would they learn subsequent novel associations
132 more easily? We also tested whether genera or sex had an impact on this ability based on
133 previous work that indicated differences in cognitive performance of gibbons were related to
134 subject-variables in that hoolock (*Hoolock leuconedys*) and siamang (*Symphalangus syndactylus*)
135 learned faster than the lar group (*Hylobates sp.*) [Cunningham et al., 2011] potentially due to
136 selection for flexibility caused by environmental variability.

137 **METHODS FOR EXPERIMENT 1**

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Ethics statement

All behavioural studies were non-invasive and subjects were fed their normal daily diet of fruits and vegetables throughout. Participation in all testing described below was voluntary on the part of the gibbons. The research adhered to the legal requirements of the USA (the country in which the research was conducted) and the research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. The research methods were also approved by the Institutional Animal Care and Use Committee of California State University, Los Angeles (IACUC protocol number 12-4). The research also had permission from the Gibbon Conservation Center (permit number 2013-1) and adhered to the ASAB Guidelines for the treatment of animals in behavioural research (2006).

Study site and subjects for Experiment 1 and 2

The gibbons were housed at the Gibbon Conservation Center (GCC), California. Some subjects had a limited history of cognitive testing previously taking part in two studies of object-mediated problem-solving tasks [Cunningham et al., 2006, 2011]. However, to the authors' knowledge, none had been exposed to any tasks similar to those reported here. The subjects in Experiment 1 consisted of 13 gibbons (age 4-14 years) with representatives from three of the four extant genera [Groves, 2002] (*Hylobates pileatus* ($N = 2$), *Hylobates moloch* ($N = 2$), *Symphalangus syndactylus* ($N = 2$), *Hoolock leuconedys* ($N = 7$)) (Table I). Ten gibbons participated in Experiment 2 (age 4-23 years), five that were also subjects in Experiment 1 plus two additional females (*H. moloch* ($N = 1$); *H. pileatus* ($N = 1$)) and one male (*H. pileatus*) that took part in Experiment 2 only (Table II). Unavoidable problems prevented the same gibbons being tested in both experiments; Violet (*H. pileatus*) was in isolation while recovering from an arm injury and a family of *H. leuconedys* moved enclosures during testing.

Gibbons were housed in outdoor enclosures (10 X 3 X 4 m) with a connected section (4 X 3 X 2.5 m) generally available at all times that could be closed off to separate subjects as required. This did not have a significant impact on the experiments as the gibbons were typically separated a few times per week when the staff cleaned the enclosures and the veterinarian checked the health of the animals. If we did notice any change in the animal's behavior that could affect their performance in testing (due to separation or other distraction), we stopped the current trial and resumed the following day. All enclosures were spaced by a minimum of 5 m and visual barriers and planted vegetation obstructed direct views between adjacent cages [see Mootnick, 1997 for more details of enclosure design]. The gibbons were fed their normal daily diet being fed five times per day with fruits and monkey biscuits in the morning and apples, bananas and greens in the afternoon. The design of the enclosures allowed the gibbons to reach their arms through fencing to access the feeding platforms used in the experiments (Figure 1).

Experiment 1

Experiment 1 consisted of two phases; Phase 1 was to determine the rank order of preferred food items (banana, cucumber and monkey biscuits) for each individual. Phase 2 assessed whether they could learn an association between their preferred foods and a color cue. In this discrimination task, the incentive was out-of-sight (concealed under a colored bucket) and we assessed how quickly the gibbons could learn to associate the position of the food reward with the cue. Three color/preferred food associations were presented consecutively, and we evaluated whether subsequent configurations were learned more efficiently suggesting gibbons were able to extract information from the first configuration to facilitate future learning. As prior studies have showed gibbons struggle with learning set formations, possibly due to short attention spans or being easily distracted, we attempted to limit these potential problems by

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focusing the gibbon’s attention on visual cues within the experiment. A video that illustrates the animals' behavior during both phases of Experiment 1 can be viewed by clicking the following link: (AJP Production Team – Please Create Link to Video 1)

Phase 1 apparatus and procedure

Before testing began, subjects were desensitized to the new feeding platform that would be used for the experimental trials. The subject’s motor skills and grasping abilities were taken into consideration when constructing the feeding platform, 130 cm long and 31 cm wide. If the platform were smaller, the gibbons would be able to easily pick it up, flip it over, and potentially lose interest in the test. If the platform were larger, it would make it difficult to transport to various enclosures. Three plastic buckets, 25 cm tall and 15 cm in diameter were painted red, yellow, and green. Three hinges were drilled into the wooden feeding platform 25 cm apart that attached the buckets open-end down, to the feeding platform. The hinges allowed the buckets to be flipped open by the gibbons to reveal food items hidden beneath (Figure 1).

To make the association between food and the feeding platform, the experimenter placed a known favorite snack (as suggested by the staff at the GCC) of pumpkin seeds and blueberries around and underneath the closed buckets on the feeding platform. This was to motivate the gibbons to touch the buckets and feel comfortable with the task of opening them to reveal the hidden food items. The experimenter presented the feeding platform to the subjects by sliding along the floor until it was aligned with the enclosure and the rewards and buckets were within the gibbons’ reach when they extended their arm through the wire mesh. The pumpkin seeds were scattered around the buckets and the buckets were closed over the blueberries. This feeding platform set-up was same on every presentation in the desensitization phase. The platform was in this position until all of the food items were consumed or for a maximum of five minutes if only

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3 207 a portion of the food was eaten. If the subject did not approach the platform at all, it was
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5 208 presented again later that same day with a gap of two hours between desensitization trials. The
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8 209 desensitization period continued on consecutive days until the subjects were comfortable using
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10 210 the feeding platform. The gibbons were assumed to associate presence of the platform with a
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12 211 reward when they readily approached, investigated and ate the pumpkin seeds, and finally
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14 212 flipped the colored buckets and ate the blueberries. On average, five presentations of the feeding
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16 213 platform were needed before there was evidence of an associative connection between the
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18 214 feeding platform and the potential for reward.
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22 215 Gibbons at GCC demonstrated preferences for specific food types when a variety of
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24 216 choices were presented. This was recognized when staff at the center brought multiple items to
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26 217 the enclosures and gibbons consistently picked and ate food in the same order. However, the
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28 218 order of preference was not the same for every gibbon, although regardless of order, they were
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30 219 usually individually consistent. As the experimental test relied on the association between
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32 220 preferred food and colored signal being learned and remembered, we first had to assess
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34 221 individual preference for the three items that would be used in the experimental tests.
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38 222 General observations indicated that favorite foods were high in sugar and bright in color
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40 223 (bananas, yams, and bell peppers). The least favorite foods had lower sugar content and were
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42 224 usually plain in appearance (monkey biscuits). For these reasons, we predicted a favorite food
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44 225 item would be banana, a moderate food item would be cucumber and the least favorite food item
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46 226 would be monkey biscuits.
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50 227 Each trial consisted of the experimenter presenting the feeding platform, within reaching
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52 228 distance of each enclosure with the food items in full view. Incentives were placed on the
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54 229 feeding platform out of view of the subjects in one of three locations that corresponded to the
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230 placement of the buckets that would be used on the test. Thus, rewards were in a horizontal line
231 relative to the enclosure fence, with the middle location being at the center of the feeding
232 platform and one reward positioned equidistant to the left and right of center. The position of the
233 three items changed in every trial in a randomly determined order. For example, on the first trial,
234 the piece of banana was on the left, cucumber in the middle and monkey biscuit on the right. For
235 the second, the position was switched so that the banana became central, cucumber right and
236 monkey biscuit left. The position of presentation was changed on every trial thereafter within the
237 constraint that the food items never appeared in the same position twice, to make sure the
238 gibbons did not get used to reaching for a particular food item in a specific direction. Notes were
239 taken of the order in which gibbons selected and ate the food items with the assumption that the
240 preferred food would be consumed first and the least preferred item, last.

241 *Phase 2 - Associative learning of color cue and preferred reward*

242 The purpose of Phase 2 was to determine if gibbons could associate colors to their rank
243 order of food items when they are out of direct sight (hidden under buckets). If the subjects were
244 able to make an association between the food items and color that signaled their preference
245 determined in Phase 1, they should select their preferred incentive as their first choice. All
246 buckets were baited with one item of the subjects preferred food (banana for all gibbons) and one
247 item of each of the other foods (cucumber and monkey biscuits) used in Phase 1 placed so that
248 when buckets were closed, the reward was out-of sight.

249 Studies using similar paradigms usually bait one location meaning the animal will only
250 receive a reward if they pick the correct cue. We chose to place a food reward under all buckets
251 and vary the ‘value’ of the food items to the individual (preferred or non-preferred) for a number
252 of reasons: 1) Sham baiting is normally employed of the non-rewarded locations to ensure the

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3 253 animals do not pick up on inadvertent experimenter-given cues during the baiting procedure
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6 254 [Garber & Dolins, 1996]. Rather than use a sham manoeuver which may still be different in
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8 255 some way to an actual baiting, we baited all buckets ensuring our actions were the same at each
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10 256 location; even though the actual placement of the rewards took place out of the subjects direct
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12 257 sight, they could potentially have monitored the experimenter's movements. 2) By including the
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14 258 two-distractor food items, we potentially increased the cognitive load by requiring subjects to
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17 259 target their preferred food from three possible food/color cue associations presented in each trial.
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20 260 3) As gibbons would be rewarded on all trials, their motivation to participate should not be
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22 261 negatively affected across repeated trials.
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24 262 Once baited, the apparatus were presented in the same way as for the food preference
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27 263 trials with the feeding platform supporting the buckets being slid along at floor level until
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29 264 aligned with the enclosure. The subjects could then extend their arms through the mesh and make
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31 265 their choice of which bucket to flip open. The first trials allowed gibbons to learn the association
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33 266 between the color cue and their preferred food item. The three colored buckets were baited out of
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36 267 direct sight of the gibbons and the apparatus presented with the three food items concealed under
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39 268 each one. On the first few presentations, the choice made would be inevitably random as the
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41 269 gibbons did not know where their favorite food item was hidden. However, with repeated trials,
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43 270 it was possible for the apes to acquire all the necessary knowledge to learn the association
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46 271 between the color cue and the value of the reward beneath it. If they learned this association,
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48 272 they should selectively choose the high value (preferred) food as their first choice on subsequent
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50 273 trials. For example, during the first trial block, if 'green' was designated as the color cue that
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53 274 would yield the highest reward, the preferred food item for the test subject (identified during
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55 275 Phase 1) would be concealed under the green bucket for all trials in that block a block consists of
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all trials needed to reach criterion before moving to a new color association to a maximum of 100). For the first trials, the position of the green bucket was held constant to allow the association between ‘green’ and the high value reward to be learned. Once the gibbon had selected the green bucket as their first choice, the position of the green cue on all remaining trials in the block was randomized; that is, the high value reward was always under the green bucket, however, the position of the green cue varied on each trial.

The subject was considered to have learned the color-reward association when they reached criterion performance set at 10 consecutive choices (out of a maximum 100 trials) of the preferred food type. Once criterion had been reached, presentations continued of the same color-reward association until all 100 trials had been given. Trials that occurred after criterion had been reached were referred to as ‘post-criterion’ trials.

Once gibbons had completed the required trials in the first block (learning and post-criterion N = 100) with the first color/reward pairing, they moved to the second block of testing where a new color/reward association had to be learned. Thus, individuals had to suppress the previously learned rule and make a new association between a colored signal and reward. Three blocks were presented (for each of the three color-reward associations to be learned) with each block consisting of 100 presentations (learning and post-criterion trials) in total. The order of presentation of each color-reward pairing was consistent across subjects. The trial was only scored if the subject showed direct interest, measured by approaching the feeding platform within 30 seconds. Trials were considered ‘correct’ if the gibbon chose the preferred item as their first choice, however, they were allowed to continue lifting buckets until all rewards were obtained (to maximize their motivation to take part). The trial was complete once all food items has been consumed or after one minute elapsed. Any additional activity after one minute was

considered “play” and the feeding platform was then taken away from the subject. If no choice was made within the minute of exposure time, the trial was marked as incomplete and would be resumed on the next day of testing. Similarly, if the subject lost interest during the trials, the experiment was stopped and resumed at a later date, continuing where the subject left off until 100 presentations were completed. The inter-trial duration was approximately three minutes. This was the time needed to change the location of the buckets into a random order and bait the buckets with the food items. Most subjects needed four sessions to complete 100 successful trial presentations; however Reg and Truman (*Hylobates sp.*) needed five sessions.

Data analysis

Data were not normally distributed and so non-parametric statistics were used to evaluate the effect of color on learning speed. Friedman’s tests assessed differences in number of trials needed to reach criterion performance (10 consecutive choices of preferred food first) for each ‘color-preferred food’ association (3 levels – Yellow, Green and Red). An extension of generalized linear models (GZLM), generalized estimating equations (GEE) that accommodates small, correlated within-subjects data sets and allows for comparisons between subjects [Garson 2013], determined how subject parameters (sex and genus) influenced learning the color-food association. As data comprised counts of trials, Poisson loglinear regression with a log link function was specified for all models with number of trials to criterion (as the response variable). Genus, sex and food-color association (consecutive choices of preferred food first) were factors in the model, with main effects tested. *Hylobates* was always the referent category for GEE parameter estimates.

For the post-criterion performance analyses (trials that occurred after the initial association had been learned), the number of trials varied across individuals due to differences in

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the acquisition of criterion performance and the maximum of 100 trials per individual summed across learning and post-criterion trials (Post-criterion trial number = Maximum number of trials (100) – number of trials to criterion). Counts were therefore transformed into percentages for the main analyses. Friedman’s tests assessed differences in number of trials where preferred food was selected first once learning had taken place for each color/preferred food association (3 levels – Yellow, Green and Red). GEE was again used to assess the retention of the color-reward association across trials in the post-criterion stage with the same factors and covariates as previously described; however, as data were no longer counts, a linear model was specified with an identity link function. Again, *Hylobates* was the reference genus for the parameter estimates. An additional Wilcoxon analysis was performed comparing the first ten trials post-criterion to the last ten to evaluate whether performance was consistent throughout trials presented. Alpha was set at 0.05 throughout and all tests were 2-tailed.

RESULTS FOR EXPERIMENT 1

Learning trials to criterion

All subjects tested demonstrated a preference for banana in the initial food choice trials with nine of the 13 subjects choosing this food item first on 100% of presentations. The remaining four subjects selected the banana first on the majority of preference trials in Phase 1 (86.67 – 93.33%) with cucumber being the occasional first choice. No subject selected monkey biscuits as first choice in the preference tests. Therefore, banana was selected as the primary color/reward referent for all subjects and responses scored as correct when the first choice made on test trials was to select the location of this food type.

The number of trials needed to learn the primary food/reward association varied across individuals (range 16-100); however, all subjects were able to reach criterion performance in all

conditions within the 100-trial maximum. The color paired with the preferred food did not influence learning speed across all individuals (Median (Yellow) = 26.00(IQR = 15.5), Median (Green) = 25.00(13.50), Median (Red) = 28.00(18.00), Freidman's test: $\chi^2(2) = 0.840$, $p = 0.657$). However, there were significant differences between the genera on acquisition of the color/reward association.

In general, *Hylobates* gibbons needed more presentations to learn the 'color-preferred food' association than either *Hoolock* or *Symphalangus* (Table III). There was a significant effect of genus on learning speed with *Hoolock* and *Symphalangus* needing significantly fewer trials than *Hylobates* to learn the color associations (GEE: *Hoolock* B = -0.677, $\chi^2(1) = 124.87$, $p < 0.001$; *Symphalangus* B = -0.854, $\chi^2(1) = 33.94$, $p < 0.001$) (Figure 3a). There were no significant differences between sexes on number of trials to criterion (GEE: B = -0.216, $\chi^2(1) = 2.854$, $p = 0.091$). Color paired with the preferred reward remained insignificant in this analysis (GEE: $\chi^2(2) = 1.965$, $p = 0.374$).

Post-criterion trials

One subject did reach criterion in the all color-reward associations, however, only on the final presentation of the green-reward configuration. This individual was therefore removed from the post-criterion performance analyses. Selection of preferred food item was generally high across all post-criterion trials (Mean (Yellow) = 91.56(SE = 1.35)%, Mean (Green) = 78.71(7.39)%, Mean (Red) = 88.51(1.88)%), with no significant differences in performance across color cues (GEE: $\chi^2(1) = 1.941$, $p = 0.379$). Sex was also non-significant as a predictor of post-criterion performance (GEE: $\chi^2(1) = 0.001$, $p = 0.970$). Genus however, did significantly impact performance with *Symphalangus* performing significantly better than *Hylobates* (B = 10.184, $\chi^2(1) = 10.468$, $p < 0.01$). *Hoolock* also obtained fewer rewards than *Symphalangus*,

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although performance was not significantly different from that of *Hylobates* subjects ($B = 4.961$, $\chi^2(1) = 1.838$, $p = 0.175$) (Figure 3b). No color/preferred food association showed diminished persistence in the first block post-criterion compared to the last block (Wilcoxon matched pairs: Yellow $Z = 0.00$, $p = 1.00$; Green $Z = -0.905$, $p = 0.366$; Red $Z = -0.707$, $p = 0.480$).

DISCUSSION FOR EXPERIMENT 1

We were able to determine the rank order of food items and the most preferred for all subjects was banana. We also determined that gibbons could successfully select their preferred food when colored buckets covered it, suggesting they could use the color as a signal to the high value food’s location. There were no differences across color-reward associations, indicating learning was not affected by the particular color/reward.

There was no evidence the gibbons tested here generalized from their learning in the first round to other rounds as there were no differences between number of trials to reach criterion performance with each successive color-reward association to be learned. Effectively, they seemed to be learning each new association from scratch – as if they had not seen or experienced the task before. This could be the result of multiple food items being used that distracted the gibbons and obscured the intended question of whether gibbons can generalize and use information learned in the first association to inform their learning in subsequent novel associations.

INTRODUCTION FOR EXPERIMENT 2

Since we found the gibbons tested showed no evidence of generalizing from their learning, we changed the methods and feeding platform in a second experiment where only one food item would be searched for with three possible locations cued by a colored background that we hoped would provide a more salient cue to the rewards location. We aimed to further

investigate the flexibility of learning by assessing whether there was any evidence of gibbons generalizing from the first color/reward association learned to other, novel associations.

In Experiment 1, gibbons were required to learn an association between a preferred food and specific color while simultaneously presented with two further possible color choices that would also provide a reward, all be it of lower value. In Experiment 2, we reduced the cognitive load by removing the secondary food items and the competing color cues in an attempt to focus the gibbon's attention on a single preferred food reward (banana). We hypothesized that by simplifying the cues presented, the gibbons tested may be better able to extract information from their initial learning experience that would aid them in subsequent novel associations: that is, they should be able to generalize from their learning in the first presentations and show improved performance in subsequent similar learning situations.

METHODS FOR EXPERIMENT 2

The feeding platform for Experiment 2 required the gibbons to reach through doors to select a hidden food item. Only one door was baited with a piece of banana and the position was determined by the color cue on the front of the platform that measured 1.2 meters long, 0.3 meters wide and 0.6m high. It was large enough for the experimenter to hide behind and "reload" the food item between trials without subjects seeing where the food item was placed. The experimenter also wore dark sunglasses during the trials to avoid giving inadvertent gaze cues to the subject.

The front of the feeding platform had three doors located at the base – on the left, center and right. The doors were six inches long and six inches wide – large enough for the animals to easily reach through (Figure 2). On the back of the doors was secured a sheet of heavy fabric that prevented the animals seeing through to the reward. Thus, in order to retrieve a reward, the

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subject had to move aside the fabric and reach through the door. Wooden dividers acted as barriers on the offside of the feeding platform, between the three possible feeding locations, to prevent the animals from reaching in one door and stretching their arms to the location of a food item behind another door. Three laminated color boards were inserted onto the front of the feeding platform behind a Plexiglas screen. The reason for the Plexiglas was because it is easily cleaned between trials and provided a mechanism to hold the interchangeable laminates in place (Figure 2). The laminates provided the color cue and varied dependent on the trial block between red, blue and yellow.

A video that illustrates the animals' behavior as well as visually displaying the experimental design of Experiment 2 can be viewed by clicking the following link: (AJP Production Team – Please Create Link to Video 2)

Desensitization and Learning Trials

Similar to Experiment 1, desensitization trials were conducted before experimental trials began. This was to desensitize the subjects to using the new feeding platform. The experimenter placed pumpkin seeds in front of the closed doors and blueberries behind the closed doors. The feeding platform was then presented to the subjects by positioning it outside the enclosure, within direct reach of the gibbons. This feeding platform set-up was exactly the same on every presentation.

Identical to Experiment 1, the platform was in this position until all of the food items were consumed or for a maximum of five minutes if only a portion of the food was eaten. The gibbons were assumed to have learned to associate the presence of the platform with a reward when they readily approached, investigated and ate the food items. If the subject did not approach the platform at all, the presenter would try again later that same day with a gap of two

437 hours between desensitization trials. The desensitization period continued on consecutive days
438 until the subjects were comfortable using the feeding platform.

439 The gibbons were recorded as associating the presence of the platform with a reward
440 when they completed two steps: 1) readily approached, investigated and ate the pumpkin seeds
441 and 2) reached through the doors and ate the blueberries. It took slightly longer for the gibbons in
442 Experiment 2 to make this association with as many as seven presentations of the feeding
443 platform required before there was evidence of an associative connection between the feeding
444 platform and the potential for reward in all gibbons. Once all subjects were consistently using the
445 new platform, we began trials to provide an opportunity for the gibbons to learn the task
446 requirements for Experiment 2.

447 During the initial learning trials, a food reward (piece of banana) was concealed behind
448 one of the doors which the gibbon was given the opportunity to retrieve. The location of the food
449 reward was determined by the color background (laminated) that was held constant to allow
450 gibbons to make the association between the reward's position and the color cue. Each subject
451 was initially presented with the red background which signified the reward (banana) was located
452 behind the left door. This configuration was repeatedly presented until the gibbon reliably chose
453 the left door, and retrieved the banana on their first selection for three consecutive trials
454 (criterion for the learning phase). Once criterion was reached for this color/position association,
455 the background color and the position of the reward were changed to a blue background with the
456 banana behind the center door, and finally a yellow background with the banana behind the right
457 door (Table II) with criterion being three consecutive correct choices for each color/reward
458 association.

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Similar to Experiment 1, a trial was only scored if the subject showed direct interest, measured by approaching the feeding platform within 30 seconds. The trial was marked as correct if the subjects’ first choice was for the rewarded location and a trial was considered complete once the food item had been consumed or after one minute elapsed (if no choice was made). Any additional activity after one minute was considered “play” and the feeding platform was then taken away from the subject. If the food item was not consumed within the minute of exposure time, the trial was marked as incomplete and would be resumed on the next day of testing. Similarly, if the subject lost interest during the trials, the experiment was stopped and resumed at a later date, continuing where the subject left off until all possible presentations were completed. The inter-trial duration for all trials (learning and experimental) was approximately three minutes.

Once criterion was reached for all three possible positions in block 1 (all trials where position of reward was always placed in accordance with the color/reward associations learned in the training trials), the subject moved on to the experimental trials (see below). On completion of the first round of testing in block 1 (learning and experimental trials), the learning trials for block 2 commenced following the same protocol as for block 1, where the position of the reward changed dependent on the color background association (block 2 - Red/Center, Blue/Right, Yellow/Left). Thus, the subject experienced a series of learning trials followed by the experimental trials for block 1, and then returned to learning trials for block 2. Once the experimental trials for block 2 were completed, the learning trials for block 3 commenced (Block 3 – Red/Right, Blue/Left, Yellow/Center).

Experimental Trials

Once the subject completed the learning trials for each block, they progressed to the experimental phase where 30 trials were presented with all three possible color/position associations for that block were presented an equal number of times across in a randomized pattern. Between each trial, the background color was changed and this determined where the reward would be placed dependent on the block. There was a similar constraint as in Experiment 1 that the position could not be the same for two consecutive trials.

For example, in block 1, the blue background signaled the food item (banana) was behind the center door, the red background, the food item was behind the left door and the yellow background, the food item behind the right door. Once all 30 experimental trials were completed, the subject went back to the learning trials for block 2 after which the experimental trials for the second block were presented. This procedure was then repeated for block 3. Overall, each individual experienced 90 experimental trials (30 for block 1, 30 for block 2 and 30 for block 3) interspersed with the relevant learning trials as described above. Scoring was the same as the learning trials.

Data analysis

Trials were scored as correct if the gibbon retrieved the food reward with their first choice when presented with the apparatus. For the learning trials, the number of trials needed to reach criterion (three consecutive correct choices) were analyzed using Friedman's repeated measures test to assess whether any background color association was more difficult to learn. GEE models were used to evaluate whether performance on the learning trials differed across genera or by sex. As data were counts, Poisson distribution with a log function was specified, genus and sex being factors in the model.

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Performance on the experimental trials was evaluated at the group and individual level.

To determine the effects of learning on subsequent color/position associations, a GEE was conducted with a binomial distribution and logit link function. Events in trials data were specified with a fixed value of 30 (number of experimental trials per block). Genus and sex were added as factors in the model with *Hylobates* as the referent category for the former.

Whether the gibbons were using the color cues to guide their choices was assessed by determining whether they were selectively choosing the correct door significantly above chance. Binomial tests with the test proportion set at 0.33 (as there were three possible choices) were conducted at the group and individual level. During the observations, a location bias seemed possible. Therefore, Chi square goodness of fit tests were used to evaluate whether the gibbons as a group and individually, were selecting any particular door (center, left or right) more that would be expected. Alpha for all tests was set at 0.05.

RESULTS FOR EXPERIMENT 2

Learning trials

Eight gibbons cooperated enough to engage in experimental trials and generate useable data. Although it was planned to include representatives from all four genera, none of the northern white-cheeked gibbons (*Nomascus leucogenys*) would participate in the experiment. Only one female white-cheeked gibbon would approach the feeding platform and remove the food items in the training trials. However, this gibbon was apprehensive to reach through the doors to remove the hidden food items in the learning or experimental trials. The male white-cheeked gibbons would not approach the feeding platform. This could be due to the daily feeding routine that involves feeding each gibbon separately with some food being handed directly or gently tossed to them to catch. They do not typically approach a feeding platform, hesitated

doing so in these experiments, which made them unwilling participants. Therefore, the final sample consists of subjects from three genera (Table I).

The number of trials needed to learn each background color/reward association ranged from 3 to 11 with most individuals reaching criterion in 5 or less trials for each color-reward configuration. There were no significant differences between number of trials to criterion for each background color association in the learning trials (Median (Yellow background) = 14.50(IQR = 6.0), Median (Blue background) = 13.00(9.0), Median (Red background) = 15.00(9.00), Freidman's test: $\chi^2(2) = 2.769$, $p = 0.250$). There was a main effect of genus on number of trials to criterion with *Hoolock* and *Symphalangus* needing fewer presentations than *Hylobates* (GEE: *Hoolock* B = -0.529, $\chi^2(1) = 99.887$, $p < 0.001$; *Symphalangus* B = -0.493, $\chi^2(1) = 31.124$, $p < 0.001$) (Figure 4). Sex was not a significant predictor of performance in the learning trials (GEE: $\chi^2(1) = 2.971$, $p = 0.085$).

Experimental trials

Consistent with the learning trials, there was no evidence that the gibbons were generalizing from the learned association in block 1 to the novel associations in block 2 and 3 (GEE: $\chi^2(2) = 0.719$, $p = 0.698$). The effect of genus on performance in the experimental trials was significant with *Symphalangus* gaining significantly more rewards than *Hylobates* (*Symphalangus* Mdn = 57.00, *Hylobates* Mdn = 43, B = 0.658, $\chi^2(1) = 65.161$, $p < 0.001$). *Hoolock* did gain more rewards than *Hylobates*, however this did not reach significance (*Hoolock* Mdn = 46, B = 0.290, $\chi^2(1) = 2.771$, $p = 0.096$). Sex was again non-significant in this analysis ($\chi^2(1) = 0.791$, $p = 0.372$).

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As a group, gibbons were selectively choosing the correct reward location above chance levels gaining 378 out of 720 possible rewards collectively (Binomial: $p < 0.001$). Individual performance is shown in Table IV, with six gibbons selecting the rewarded door significantly above chance overall. Within this group, three gibbons dropped below chance level on one set of the three with the remaining three performing above chance in all sets. Developing a bias for one location over the others may have influenced performance. Five of the eight gibbons showed a positional bias (Table V) selectively favoring the center door in general. This bias did not however emerge consistently across all blocks.

GENERAL DISCUSSION

In Experiment 1, we found no evidence the gibbons tested generalized from their learning and we cautioned this could be the result of multiple food items and competing color cues being used that distracted the gibbons. Therefore, we changed the experimental design to a more specific task in Experiment 2 to focus the gibbon’s attention on a single food/color association to see if the gibbons were able to use information from their first learning experience of the task to facilitate future learning of novel color/reward associations. Despite making these changes, the data show they learned each new association from scratch – as if they had not seen or experienced the task before as in Experiment 1. Our findings are similar to other studies [Rumbaugh & McCormack, 1967] that found gibbons struggle with learning set formation and do not show the learning to learn pattern as found in other species. However, once the learning association was made, the gibbons performed well above chance. We found no differences across color associations indicating learning was not affected by the particular color / reward association

The results reported here could be due to the small sample size and because of the captive environment in which these gibbons were raised. Karenina and Marlow, siamang gibbons (*Symphalangus syndactylus*) who performed quite well in the tasks reported here, had a lot of human interaction from a young age. Perek, a Javan gibbon (*Hylobates moloch*) who did not perform as well in these experiments, was born at Howlets Wild Animal Park, UK, and did not have as much human interaction.

The Gibbon Conservation Center provided a unique opportunity being the only institution in the world to house and breed all four genera of gibbon [Mootnick, 1997]. However, obtaining large sample sizes is very challenging as there are very few gibbons (particularly of the *Hoolock* genus) in captivity. Another possibility for these results is the low criterion level set for Experiment 2. We lowered the number of consecutive correct learning trials to compensate for the gibbons short attention spans but this may not have given them sufficient time to really learn the association. Results from previous experiments where hundreds of trials have been presented in the learning phase [Rumbaugh & McCormack, 1967] suggest performance may have been much better had they been given more opportunity to learn. Despite such a low criterion, many of the gibbons did perform well above chance in the experimental trials although they may not have had the opportunity to learn the rules of the task that could then be generalized to future novel presentations.

We found a key difference in the learning and association rates between male and female gibbons with the males learning at a faster rate than females. Reproductively active females may be highly motivated to explore potential resources due to the additional energy requirements of pregnancy and lactation; however, increased investment in developing offspring could make them more guarded in their investigations and so reluctant to engage with unknown objects such

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as our testing equipment [Cunningham et al., 2011]. Males, without the investment in offspring, may be more devoted to the search of potential resources and more willing to explore novel objects.

We have shown that when given provisioned food items, the subjects tested have preferred foods and can associate color signals with these foods. However, there were no differences across color associations and the rate of learning was no different from the colors red, green, yellow, blue, or if the food item was on the left, center or right. This suggests the subjects can associate each of the colors tested to the food items at the same rate and accuracy with no particular preference to a specific color or location.

The *Hylobates* sp. had the slowest learning rate before they made the association between their preferred foods and the color cue in Experiment 1 and 2. *Hoolock* learned the association significantly quicker, needing fewer trials in all color/preferred food association learning phases. For all gibbons tested, males learned faster than the females, however age did not impact learning rate although younger gibbons did show more inconsistencies in their performance, selecting other food items as their first choice on some trials in Experiment 1, especially in the post-criterion phase. This however did not have a significant impact on results with all subjects selecting their preferred food item with a high level of accuracy in all post-criterion trials.

Possible Foraging Implications

This ability to associate colors to preferred foods can be an advantage in a changing environment. For instance, *Hoolock* gibbons, which performed well compared to the lar-group in this study, are from an environment that is variable and resources can be scarce. The lar-group gibbons, who performed the poorest, live in an area where the climate is more stable and food is likely to be plentiful year round [Brockman & van Schaik CP, 2005; Curran & Leighton, 2000].

This suggests that animals required to search more vigorously for high quality food items due to environmental variability are more flexible in their learning than animals that do not have the same foraging pressures.

There have been previous investigations that support the assumption that trichromatic color vision provides an advantage related to foraging [Caine & Mundy, 2000; Nagle & Osorio, 1993; Osorio & Vorobyev, 1996; Regan et al., 1998, 2001; Lucas et al., 1998]. However, these investigations did not take into account using colors as visual landmarks or make the direct connection between preferred foods and how animals can associate colors to these foods.

To consider possible foraging implications as well as the ecological validity of the experimental design and results reported here, the fact that color is an ephemeral cue in the environment must be taken into account. In general, forests retain a homogenous set of colors with changes in accordance with fruit ripening and leave leaf maturation across time. Mostly, animals focus on more permanent environmental cues while navigating such as the size and shape of trees. However, if an animal can take advantage of the changing colors in the environment and learn to make the association of these new color cues to the location of ripe fruit, they will have a foraging advantage over animals that do not possess this ability.

Resource availability is rarely ideal. Research has found yearly fluctuations in the availability of resources which has a significant impact on the demography, foraging ecology, life history patterns, population density, anti-predator strategies, and social behaviour of nonhuman primates [Brockman & van Schaik, 2005]. When preferred foods are scarce, optimal foraging theory predicts primates should attempt to maintain the net energy intake required for physiological maintenance by either increasing their ranges to continue utilizing preferred foods or relying on alternative foods [e.g., MacArthur & Pianka, 1966; Stephens & Krebs, 1986; van

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Schaik & Brockman, 2005]. Thus, primates may act as “energy maximizers,” increasing their day journey length (DJL) or home range size to consume as many scarce preferred resources as possible, or “energy minimizers,” decreasing their DJL and home range size while consuming more low-quality resources [e.g., Clutton-Brock, 1977; Boinski, 1987; Barton et al., 1993; Barton, 1998, 1999; Overdorff, 1993; Hemingway & Bynum, 2005; Riley, 2007].

Given a gibbon’s body size, morphological and physiological adaptations, grouping patterns and social organization, they fit the description of energy maximizers. They spend a great deal of energy searching for and traveling between patches of foods. They use their adaptations, expand their ranges, and continue to search for preferred foods that are usually high-energy fruits that are bright in color. In order understand the foraging advantages conferred by the ability to associate ephemeral color cues to preferred food items in relation to resource distribution, further testing is needed in both captivity and nature.

Conclusions and Future Study

Since we have shown the gibbons tested had difficulty generalizing from their learning in one context and using it to facilitate learning in a similar situation, we must conclude that these apes are capable of making color/reward associations but cannot use their learning flexibly. This makes it unlikely that they would, with further testing, demonstrate learning set formation consistent with results from earlier research [Rumbaugh & McCormack, 1967]. However, the emergence of learning to learn patterns may occur with the use of more structured small steps to facilitate learning of the rules of the task in an incremental way. For example, repeated presentations of one color cue that signifies a reward presented with a neutrally colored unreinforced cue before changing the color cue but not the rule (color would still indicate the position of the reward) after the subject experienced many more trials than used here may allow

gibbons to extract the general rule that can be used to solve future novel presentations rather than just a simple stimulus-reward association. With this more intensive training regime, they may be able to apply their learning in a more flexible way.

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Figure Legends

Figure 1. Betty (Female *H. leuconedys*) engaged in Experiment 1. The gibbons reached through the fencing and flipped open the buckets to reveal the food items. The buckets were drilled in place with hinges that allowed them to be easily flipped and replaced to the different sets.

Figure 2. Feeding platform used for Experiment 2. This platform required the gibbons to reach through doors to select the hidden food item. Three laminated color boards were inserted onto the front of the feeding platform behind a Plexiglas screen.

Figure 3: Adjusted means for number of trials needed to reach criterion performance (10 consecutive first choices of preferred food type) by genus (a) and percentage of correct responses by genus in the post-criterion phase (b). Error bars represent $\pm 1SE$. ** denotes significance at $p < 0.001$

Figure 4: Adjusted means for number of trials to reach criterion performance in the learning trials of Experiment 2 by genus. Error bars represent $\pm 1SE$. ** denotes significance at the 0.001 level.

Tables:

Table I. Names, species, sex, and age of the subjects in Experiment 1 and Experiment 2.

Subject	Species	Sex	Age in yrs	Experiment
Marlow	<i>Symphalangus syndactylus</i>	Female	8	1 & 2
Karenina	<i>Symphalangus syndactylus</i>	Female	14	1 & 2
Khin Maung Win	<i>Hoolock leuconedys</i>	Male	5	1 & 2
U Myint Swe	<i>Hoolock leuconedys</i>	Male	4	1 & 2
Hmawe Ni	<i>Hoolock leuconedys</i>	Female	11	1 & 2
Betty	<i>Hoolock leuconedys</i>	Female	14	1
Chan Thar	<i>Hoolock leuconedys</i>	Female	6	1
U Maung Maung	<i>Hoolock leuconedys</i>	Male	12	1
Win Bo	<i>Hoolock leuconedys</i>	Male	10	1
Reg	<i>Hylobates moloch</i>	Male	13	1
Perak	<i>Hylobates moloch</i>	Male	11	1
Truman	<i>Hylobates plieatus</i>	Male	10	1
Violet	<i>Hylobates pileatus</i>	Female	4	1
Tuk	<i>Hylobates pileatus</i>	Female	20	2
Chloe	<i>Hylobates moloch</i>	Female	23	2
Domino	<i>Hylobates pileatus</i>	Male	18	2

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Table II: Experimental sets used in Experiment 1 and 2.

Sets	Experiment 1 ¹	Experiment 2 ²
1	Red left, yellow center, green right	Red left, blue center, yellow right
2	Red left, green center, yellow right	Blue right, yellow left, red center
3	Yellow left, red center, green right	Yellow center, red right, blue left
4	Yellow left, green center, red right	
5	Green left, red center, yellow right	
6	Green left, yellow center, red right	

¹For Experiment 1, color refers to the bucket covering the food and position (left, right, center) designates the position of the colored bucket on the feeding platform.
²In Experiment 2, the color refers to the background and the position to the location of the food reward.

Table III: Unadjusted means for number of trials to criterion performance.

Preferred food color association¹	<i>Hoolock</i> (n = 7) mean(SE)	<i>Hylobates</i> (n = 4) mean(SE)	<i>Symphalangus</i> (n = 2) mean(SE)
YELLOW	22.29(1.782)	50.25(11.161)	29.50(10.500)
GREEN	28.57(2.277)	48.50(19.294)	23.00(0.000)
RED	27.14(2.064)	48.75(11.116)	21.00(0.000)

¹Ten consecutive correct choices for three genera of gibbon for each color-preferred food association in Experiment 1

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Table IV: Number of correct responses in the experimental trials of Experiment 2.

Subject	S1		S2		S3		Total	
	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>
Marlow	19	0.001***	19	0.001***	18	0.002**	56	0.001***
Khin	15	0.001***	12	0.002	11	0.001	38	0.042
Maung Win								
U Myint	16	0.017*	21	0.001***	19	0.002**	56	0.001***
Swe								
Karenina	23	0.001***	19	0.002**	16	0.017*	58	0.001***
Hmawe Ni	16	0.017**	14	0.017	16	0.017**	46	0.001***
Chloe	14	0.017	15	0.001***	16	0.017**	45	0.001***
Domino	11	0.001	11	0.001	14	0.017	36	0.017
Tuk	15	0.001***	12	0.263	16	0.017**	43	0.003**

Across each set (maximum correct is 30 trials per set), and in total (maximum score is 90 trials) and binomial test results. Values noted as significant represent performance above chance level. P values that are significant but not annotated represent performance below chance levels.

*significant at the 0.05 level
**significant at the 0.01 level
***significant at the 0.001 level

Table V: Chi square tests to evaluate individual positional bias on experimental trials of Experiment 2.

Subject	S1		S2		S3		Total	
	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>
Marlow	4.200	0.122	6.200	0.045*	4.200	0.122	14.067	0.001***
Khin Maung Win	4.200	0.122	3.800	0.150	1.800	0.407	4.067	0.131
U Myint Swe	9.800	0.007**	7.800	0.020*	9.800	0.007**	26.467	0.001***
Karenina	0.200	0.905	3.800	0.150	15.800	0.001***	13.867	0.001***
Hmawe Ni	3.800	0.150	4.200	0.122	32.00	0.202	9.624	0.008*
Chloe	0.600	0.439	0.133	0.715	13.400	0.001***	13.867	0.001***
Domino	6.200	0.045*	- ^a	- ^a	2.600	0.273	4.467	0.107
Tuk	1.400	0.497	11.400	0.003**	3.800	0.150	10.400	0.006**

Significant values denote a deviance from the expected values of 10 choices at each location. For all gibbons with a bias, it was for the center door.

^a observed and expected values were the same therefore Chi square was not calculated

*significant at the 0.05 level

**significant at the 0.01 level

***significant at the 0.001 level



Figure 1. Betty (Female *H. leuconedys*) engaged in Experiment 1. The gibbons reached through the fencing and flipped open the buckets to reveal the food items. The buckets were drilled in place with hinges that allowed them to be easily flipped and replaced to the different sets.
152x86mm (220 x 220 DPI)

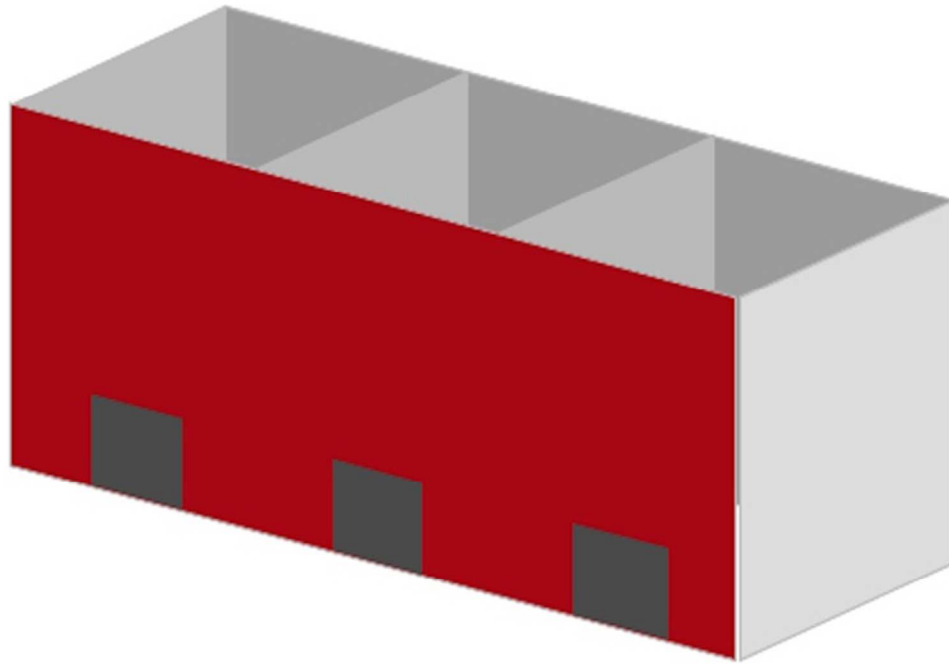


Figure 2. Feeding platform used for Experiment 2. This platform required the gibbons to reach through doors to select the hidden food item. Three laminated color boards were inserted onto the front of the feeding platform behind a Plexiglas screen.
246x166mm (72 x 72 DPI)

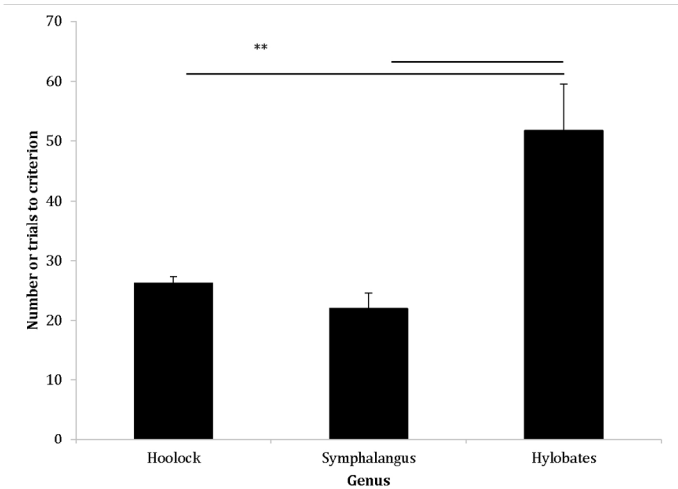
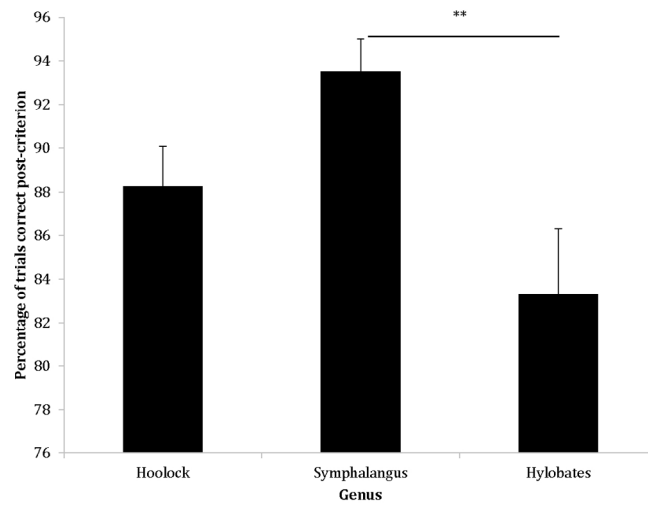


Figure 3: Adjusted means for number of trials needed to reach criterion performance (10 consecutive first choices of preferred food type) by genus (a) and percentage of correct responses by genus in the post-criterion phase
215x279mm (200 x 200 DPI)



(b). Error bars represent $\pm 1SE$. ** denotes significance at $p < 0.001$
215x279mm (200 x 200 DPI)

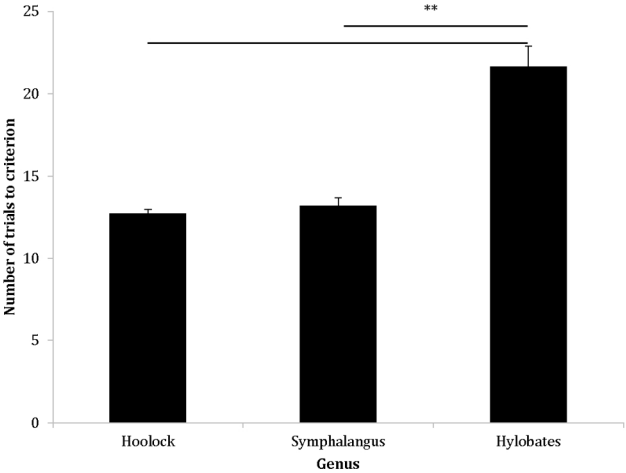


Figure 4: Adjusted means for number of trials to reach criterion performance in the learning trials of Experiment 2 by genus. Error bars represent $\pm 1SE$. ** denotes significance at the 0.001 level.

215x279mm (200 x 200 DPI)